

# ON A LINK BETWEEN A SPECIES SURVIVAL TIME IN AN EVOLUTION MODEL AND THE BESSEL DISTRIBUTIONS

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**ABSTRACT.** We consider a stochastic model for species evolution. A new species is born at rate  $\lambda$  and a species dies at rate  $\mu$ . A random number, sampled from a given distribution  $F$ , is associated with each new species at the time of birth. Every time there is a death event, the species that is killed is the one with the smallest fitness. We consider the (random) survival time of a species with a given fitness  $f$ . We show that the survival time distribution depends crucially on whether  $f < f_c$ ,  $f = f_c$  or  $f > f_c$  where  $f_c$  is a critical fitness that is computed explicitly.

## 1. INTRODUCTION

Consider a stochastic model for species evolution in which a new species is born at rate  $\lambda$  and an existing species dies at rate  $\mu$ . A random number, sampled from a given distribution  $F$ , is associated with each new species at the time of birth. We think of the random number associated with a given species as being the *fitness* of the species. These fitnesses are independent of each other and of everything else in the process. Every time there is a death event, the species that is killed is the one with the smallest fitness. We assume  $F$  to be an

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absolute continuous distribution function. In this paper we study the survival time of a given species with fitness  $f$ . We show that there is a critical fitness  $f_c$  and a sharp phase transition for the survival time of the species. Our analysis is based on a closed connection between our model and random walks.

A similar model, meant to build phylogenetic trees, was introduced in Liggett and Schinazi [7]. A discrete version of this model is studied in Guiol *et al* [6] where a phase transition is shown.

## 2. MAIN RESULTS

Recall we assume that  $F$  is an absolute continuous distribution function. This implies that there exists a probability density  $\varphi$  on  $\mathbb{R}$  such that

$$F(x) = \int_{-\infty}^x \varphi(u) \, du.$$

Denote  $\text{Supp}(F)$  the support of distribution  $F$ :

$$\text{Supp}(F) = \{x \in \mathbb{R} : \varphi(x) > 0\}$$

Assume that originally there are  $k$  species in the process, with associate fitness  $f_1 < f_2 < \dots < f_k = f$  in the support of  $F$ . Denote  $\tau_f^k$  the r.v corresponding to the survival time of the species with fitness  $f$  in that context.

**Theorem 2.1.** *The survival time  $\tau_f^k$  has a Bessel distribution :*

$$\mathbb{P}(\tau_f^k > t) = 1 - \left(\frac{\mu}{\lambda_f}\right)^{k/2} \int_0^t e^{-(\mu+\lambda_f)u} \frac{k}{u} I_k(2\sqrt{\mu\lambda_f} u) \, du \quad (2.1)$$

with  $\lambda_f := \lambda F(f) < \lambda$  and where  $I_k$  is the modified Bessel function of the first kind with indice  $k$  defined by

$$I_k(x) = \sum_{\ell=0}^{+\infty} \frac{1}{(\ell+k)!\ell!} \left(\frac{x}{2}\right)^{2\ell+k}. \quad (2.2)$$

**Remark 2.2.** Devroye [3, chapter IX section 7 p.470] includes distribution (2.1) among the class of Bessel function distributions. One can also find it in Feller [4, chapter II section 9 Problem 15 p.65] without a specific name.

**Remark 2.3.** The survival time  $\tau_f^k$  is not affected by living species with fitness above  $f$ .

**Remark 2.4.** Whenever  $\lambda_f \leq \mu$ ,  $\tau_f^k$  has probability density

$$\varphi_\tau(t) = \left(\frac{\mu}{\lambda_f}\right)^{k/2} e^{-ct\frac{k}{t}} I_k(2\sqrt{\mu\lambda_f} t) \text{ for } t > 0.$$

In the case  $\lambda_f > \mu$  the previous function is not a density probability since

$$\int_0^\infty \left(\frac{\mu}{\lambda_f}\right)^{k/2} e^{-ct\frac{k}{t}} I_k(2\sqrt{\mu\lambda_f} t) dt = \left(\frac{\mu}{\lambda_f}\right)^{k/2} \left(\frac{\mu}{\lambda_f}\right)^{k/2} = \left(\frac{\mu}{\lambda_f}\right)^k < 1$$

Though formula (2.1) gives the exact distribution of the survival time, it is not straightforward to come to a conclusion from it. Next result sheds light in the phase transition property of our model.

**Corollary 2.5.** *With the previous notation*

(a) *If  $\lambda_f < \mu$  then*

$$\mathbb{P}(\tau_f^k > t) \sim C_k \frac{e^{-\gamma t}}{t^{3/2}}$$

with  $C_k = \frac{k}{2\sqrt{\pi}} \left( \frac{\mu}{\lambda_f} \right)^{k/2} (\mu\lambda_f)^{-1/4} (\sqrt{\mu} - \sqrt{\lambda_f})^{-2}$  and  $\gamma = (\sqrt{\mu} - \sqrt{\lambda_f})^2$ .

(b) If  $\lambda_f > \mu$  then

$$\begin{aligned} \mathbb{P}(\tau_f^k = +\infty) &= 1 - \left( \frac{\mu}{\lambda_f} \right)^k; \\ \mathbb{P}(+\infty > \tau_f^k > t) &\sim C_k \frac{e^{-\gamma t}}{t^{3/2}}. \end{aligned}$$

(c) If  $\lambda_f = \mu$  then

$$\mathbb{P}(\tau_f^k > t) \sim k(\pi\mu t)^{-1/2}.$$

**Remark 2.6.** Note, from Corollary 2.5, that if  $\lambda > \mu$  there is a phase transition in  $f$ . A species born with a fitness lower than

$$f_c := F^{-1}(\mu/\lambda) \tag{2.3}$$

dies out exponentially fast while a species with a fitness greater than  $f_c$  has a positive probability of surviving forever. The larger  $\lambda/\mu$  (recall that  $F^{-1}$  is non-decreasing) the more welcoming the environment is to new species. If  $\lambda/\mu < 1$  all species will die exponentially fast. On the other hand if  $\lambda/\mu$  is large then even species with relatively low fitness will make it.

Up to now we have discussed the survival of a species with a given fitness  $f$ . It is particularly relevant to derive some information about the distribution of these surviving species. Suppose that  $\lambda > \mu$  and let  $L_t$  and  $R_t$  be the sets of species alive at time  $t$  whose fitness is

respectively lower than  $f_c$  and higher than  $f_c$ . Since each fitness that has appeared up to time  $t$  will not show up again a.s., we can identify each species with its fitness and think of  $L_t$  and  $R_t$  as sets of points in  $(-\infty, f_c)$  and  $(f_c, \infty)$  respectively. Next result states a straightforward application of the main result of Guiol *et al* [6]

**Proposition 2.7.** *Suppose that  $\lambda > \mu$ . Then*

(a) *The number  $|L_t|$  of species whose fitness is below  $f_c$  is a null recurrent birth and death process. In particular, the set  $L_t$  is empty infinitely often with probability one.*

(b) *Let  $f_c < a < b$  then*

$$\lim_{t \rightarrow \infty} \frac{1}{t} |R_t \cap (a, b)| = \frac{\lambda(F(b) - F(a))}{\lambda + \mu} \text{ a.s.}$$

*Proof of Proposition 2.7.* To see this observe that the embedded discrete Markov chain for our process is the *stochastic model of evolution* defined in Guiol *et al* [6] in such a way that  $p = \lambda/(\lambda + \mu)$ . Consider that whenever the total number of species is 0, the death marks (see page 7 below) in the construction of the process are ignored so the total number of species stays 0 with probability  $\mu/(\lambda + \mu)$ .  $\square$

**Remark 2.8.** Observe that from Ben Ari *et al.* [2] it would be also possible to get a Central Limit Theorem and a Law of the Iterate logarithm for  $R_t$ .

## 3. PROOFS

**3.1. Construction of the process.** The construction uses ideas from Harris Graphical method for Markov Processes and basically take advantage from projections properties of a bi-dimensional Poisson process with rate 1. In the sequel we construct a bi-variate process  $Z_t = (Z_t^1, Z_t^2)$  in which  $Z_t^1$  will represent the number of living species at time  $t$ , and  $Z_t^2$  will be the set of associated living fitness: In particular  $|Z_t^2| = Z_t^1$ , where  $|A|$  denotes the cardinal of set  $A$ .

Let  $M$  be a two dimensional Poisson process with rate 1 on  $\mathbb{R}^+ \times \mathbb{R}$ . For notational convenience we will identify the  $x$ -line of the plane as the time line.

Suppose we start the process with  $k \geq 1$  species, let  $f_1, \dots, f_k$  be  $k$  independent random variables with  $F$  distribution, independent from  $M$ .

Let  $T_0 = 0$  and  $Z_0 = (Z_0^1, Z_0^2) = (k, \{f_1, \dots, f_k\}) \in \mathbb{N} \times \mathbf{S}$  where  $\mathbf{S}$  is the set of finite subsets of real numbers in  $[0, 1]^{\mathbb{N}}$ .

Define

$$T_1 = \inf\{t > 0 : M([0, t] \times [0, \lambda + \mu]) > 0\} \quad (3.1)$$

that is the first time  $t \in \mathbb{R}^+$  that a Poisson mark falls into the strip  $\mathbb{R}^+ \times [0, \lambda + \mu]$ . Denote by  $(T_1, Y_1)$  the coordinate of the Poisson mark realizing the infimum in (3.1). Observe that from the Poisson process properties  $Y_1$  is a uniform  $[0, 1]$  r.v. independent of  $T_1$ .

- Whenever  $Y_1 \in [0, \lambda]$  then let  $f_{k+1} = F(Y_1/\lambda)$  (observe that  $f_{k+1}$  is also a r.v. with  $F$  law and independent of  $T_1$ ) and let

$$Z_{T_1} = (Z_0^1 + 1, Z_0^2 \cup \{f_{k+1}\}) = (k + 1, \{f_0, \dots, f_{k+1}\})$$

this will represent the birth of a new species;

- else, whenever  $Y_1 \in ]\lambda, \lambda + \mu]$ , let

$$Z_{T_1} = (Z_0^1, Z_0^2 \setminus \min\{Z_0^2\}) = (k - 1, \{f_0, \dots, f_k\} \setminus \min\{f_i : 1 \leq i \leq k\})$$

this will represent the death of the weakest species.

For all  $t \in [0, T_1[$  denote  $Z_t = Z_0$ . We have thus construct the process  $Z_t$  until time  $T_1$  (included).

For all  $n \geq 1$  denote by  $T_n$  the time of the  $n$ -th mark of the Poisson process  $M$  in the strip  $\mathbb{R}^+ \times [0, \lambda + \mu]$  that is

$$T_n = \inf\{t > T_{n-1} : M([0, t] \times [0, \lambda + \mu]) > 0\}.$$

Suppose the process  $Z_t$  is construct up to time  $T_n$ ,  $n \geq 1$ . As before denote by  $(T_{n+1}, Y_{n+1})$  the coordinate of the  $n + 1$ st Poisson mark.

- Whenever  $Y_{n+1} \in [0, \lambda]$  then let  $f_{k+n+1} = F(Y_{n+1}/\lambda)$  and define

$$Z_{T_{n+1}} = (Z_{T_n}^1 + 1, Z_{T_n}^2 \cup \{f_{k+n+1}\})$$

- else

$$Z_{T_{n+1}} = (Z_{T_n}^1 - \mathbf{1}_{\{Z_{T_n}^1 > 0\}}, Z_{T_n}^2 \setminus \min\{Z_{T_n}^2\}).$$

with the convention  $\min \emptyset = \emptyset$ ;

then for all  $t \in [T_n, T_{n+1}[$  let  $Z_t = Z_{T_n}$ .

So by induction one can construct the process  $(Z_t)_{t \geq 0}$  so that the second coordinate of  $Z_t$  i.e.  $Z_t^2$  represents our fitness process starting with  $k$  species.

**3.2. An useful coupling.** From the previous construction one can couple  $Z_t = (Z_t^1, Z_t^2)$  with another process  $X_t \in \mathbb{N}$  as follows.

Let  $X_0 = Z_0^1$  (with the construction's notation) and denote by  $f = \max\{f_1, \dots, f_k\}$ . At time  $T_1$

- if  $Y_1 \in [0, \lambda_f] \cup ]\lambda, \lambda + \mu]$  then let  $X_{T_1} = Z_{T_1}^1$ . Observe that this corresponds to a simultaneous death or to a simultaneous birth with associate fitness less than  $f$  for the  $Z$  process;
- else (when  $Y_1 \in ]\lambda_f, \lambda]$ ) then let  $X_{T_1} = X_0$ . In this case there is a birth on the  $Z$  process with associate fitness bigger than  $f$  and nothing for the  $X$  process.

As before define  $X_t = X_0$  for all  $t \in [0, T_1[$ .

For all set  $A$  of numbers in  $[0, 1]$  denote by

$$\phi_f(A) = \{x \in A : x \leq f\}, \quad (3.2)$$

i.e. the set of numbers in  $A$  less or equal to  $f$ .

Observe that  $X_t = Z_t^1$  on  $[0, T_1[$ ,  $X_{T_1} = |\phi_f(Z_{T_1}^2)| \leq Z_{T_1}^1$ .

For  $n \geq 1$  suppose that  $X_t$  is construct up to time  $T_n$ .

If  $X_{T_n} \neq 0$  then  $|\phi_f(Z_{T_n}^2)| = X_{T_n}$



- if  $Y_{n+1} \in [0, \lambda_f]$  (recall that  $f_{k+n+1} := F(Y_{n+1}/\lambda) \leq f$ ) define

$$X_{T_{n+1}} = X_{T_n}^1 + 1,$$

- if  $Y_{n+1} \in [\lambda, \lambda + \mu]$  then define

$$X_{T_{n+1}} = X_{T_n}^1 - 1$$

- else let  $X_{T_{n+1}} = X_{T_n}$ ;

In case  $X_{T_n} = 0$  let  $X_{T_{n+1}} = 0$ .

This defines a random sequence  $(T_n, X_{T_n})_{n \geq 0}$ , we define the process  $(X_t)_{t \geq 0}$  as  $X_t = X_{T_n}$  for all  $t \in [T_n, T_{n+1}[$ .

The proof of Theorem 2.1 relies on the following Lemma.

**Lemma 3.1.** *For any  $k \geq 1$*

$$\{\tau_f^k > t\} = \{X_t > 0\} \quad (3.3)$$

*i.e.  $\tau_f^k$  has the same law as the first passage time to 0 of  $X_t$  the simple Bernoulli random walk starting at  $k$  with rate  $c = \lambda_f + \mu$  and individual steps equal to 1 or  $-1$  with respective probability  $p = \lambda/c$  and  $q = \mu/c$ .*

*Proof of Lemma 3.1.* We have  $X_0 = Z_t^1 = |\phi_f(Z_t^2)| = k > 0$ . From the construction for all  $t < \tau_f^k$  we have  $\min Z_t^2 \leq f$  this implies  $X_t > 0$ . Conversely if  $\tau_f^k \leq t$  as  $\min Z_{\tau_f^k}^2 > f$  this implies  $X_{\tau_f^k} = 0$  and thus  $X_t^1 = 0$ .  $\square$

*Proof of Theorem 2.1.* Let  $(T_n)_{n \geq 1}$  denotes the jump times of the process  $(X_t)_{t \geq 0}$  and set  $T_0 = 0$ . The random sequence  $(X_{T_n})_{n \geq 0}$  is a simple

discrete time random walk on  $\mathbb{N}$  with individual steps equal to 1 or  $-1$  with respective probability  $p$  and  $q$ . Denote by  $H_0$  the first hitting time of 0 of this walk. A standard computation (see for instance Grimmett-Stirzaker [5, (15) p.79]) gives

$$\mathbb{P}(H_0 = n | X_0 = k) = \frac{k}{n} \binom{n}{(n+k)/2} q^{(n+k)/2} p^{(n-k)/2}$$

whenever  $n+k$  is even, 0 otherwise. As  $T_n$  has a Gamma distribution with parameters  $c$  and  $n$  this implies that

$$\begin{aligned} \mathbb{P}(X_t = 0) &= \int_0^t \sum_{n=k}^{\infty} \frac{c^n}{(n-1)!} u^{n-1} e^{-cu} \mathbb{P}(H_0 = n | X_0 = k) du \\ &= \int_0^t e^{-cu} \frac{k}{u} \sum_{n=k}^{\infty} \frac{1}{n!(n-k)!} (cu)^{2n-k} q^n p^{n-k} du \\ &= \int_0^t e^{-cu} \frac{k}{u} \sum_{\ell=0}^{\infty} \frac{1}{(\ell+k)! \ell!} (cu)^{2\ell+k} q^{\ell+k} p^{\ell} du \\ &= \int_0^t e^{-cu} \frac{k}{u} \left(\frac{q}{p}\right)^{k/2} \sum_{\ell=0}^{\infty} \frac{1}{(\ell+k)! \ell!} (cu\sqrt{pq})^{2\ell+k} du \end{aligned}$$

and from the definition of the Bessel function (2.2)

$$\mathbb{P}(X_t = 0) = \int_0^t e^{-cu} \frac{k}{u} \left(\frac{q}{p}\right)^{k/2} I_k(2cu\sqrt{pq})$$

□

**Remark 3.2.** Let  $\tau_f^0 = 0$  We have

$$\tau_f^k = \sum_{j=1}^k \tau_f^j - \tau_f^{j-1}.$$

Observe that  $\tau_f^k$  are a.s. finite stopping times and from the Strong Markov property  $(\tau_f^j - \tau_f^{j-1})_{1 \leq j \leq k}$  is an i.i.d. sequence of r.v. with the distribution of  $\tau_f := \tau_f^1$ .

As observed in Remark 2.4  $\lambda_f < \mu$  the expression (2.1) gives the density probability of  $\tau_f$ :

$$\varphi_{\tau_f}(t) = \sqrt{\frac{\mu}{\lambda_f}} e^{-(\mu+\lambda_f)t} \frac{1}{t} I_1(2\sqrt{\mu\lambda_f}t)$$

for  $t > 0$ . Which allows to compute its Moment Generating Function:

$$M(s) = \mathbf{E}(e^{-\tau_f s}) = \frac{2\mu}{\sqrt{(s + \mu + \lambda_f)^2 - 4\mu\lambda_f} + s + \mu + \lambda_f}.$$

This in turns allows us to compute  $\mathbf{E}(\tau_f) = \frac{2\mu}{\mu - \lambda_f}$ . So that one can see easily that

$$\mathbf{E}(\tau_f^k) = k \frac{2\mu}{\mu - \lambda_f}$$

for all  $k \geq 0$ .

*Proof of Corollary 2.5 (a).* When  $\lambda_f < \mu$  (2.1) reads

$$\mathbb{P}(\tau_f > t) = \left(\frac{\mu}{\lambda_f}\right)^{k/2} \int_t^{+\infty} e^{-(\mu+\lambda_f)u} \frac{k}{u} I_k(2\sqrt{\mu\lambda_f}u) du$$

Since (see Arfken and Weber, of [1, section 11.6 eq.11.137 p.719]) for all  $k \geq 1$

$$\frac{e^x}{\sqrt{2\pi x}} \left(1 - \frac{4k^2 - 1}{8x}\right) \leq I_k(x) \leq \frac{e^x}{\sqrt{2\pi x}} \quad (3.4)$$

for  $x$  large enough,

$$\begin{aligned} & \frac{1}{2\sqrt{\pi}(\mu\lambda_f)^{1/4}} \frac{e^{-(\sqrt{\mu}-\sqrt{\lambda_f})^2 u}}{u^{3/2}} \left(1 - \frac{4k^2 - 1}{16\sqrt{\mu\lambda_f} u}\right) \\ & \leq \frac{e^{-(\mu+\lambda_f)u}}{u} I_1(2\sqrt{\mu\lambda_f} u) \leq \\ & \frac{1}{2\sqrt{\pi}(\mu\lambda_f)^{1/4}} \frac{e^{-(\sqrt{\mu}-\sqrt{\lambda_f})^2 u}}{u^{3/2}}, \end{aligned} \quad (3.5)$$

also for  $x$  large enough. Denoting  $\gamma = (\sqrt{\mu} - \sqrt{\lambda_f})^2$ , observe that

$$\left( \frac{1}{\gamma} \frac{1}{t^{3/2}} - \frac{4k^2 - 1}{2\gamma^2} \frac{1}{t^{5/2}} \right) e^{-\gamma t} \leq \int_t^{+\infty} \frac{e^{-\gamma u}}{u^{3/2}} du \leq \frac{1}{\gamma} \frac{e^{-\gamma t}}{t^{3/2}}. \quad (3.6)$$

Thus

$$\int_t^{+\infty} \frac{e^{-\gamma u}}{u^{3/2}} du \sim \frac{1}{\gamma} \frac{e^{-\gamma t}}{t^{3/2}},$$

so we have a sharp asymptotic estimate for the integral of the upper bound in (3.5).

For the integral of the lower bound, denoting  $\alpha = (4k^2 - 1)/(16\sqrt{\mu\lambda_f})$ , just observe that

$$\int_t^{+\infty} \left(1 - \frac{\alpha}{u}\right) \frac{e^{-\gamma u}}{u^{3/2}} du \geq \int_t^{+\infty} \frac{e^{-\gamma u}}{u^{3/2}} du - \frac{\alpha}{\gamma} \frac{e^{-\gamma t}}{t^{5/2}} \quad (3.7)$$

to see that we also have a sharp asymptotic estimate for the integral of the lower bound in (3.5). Besides, both asymptotic estimates agree.

Plugging (3.7) and (3.6) into (3.5) and then into (2.1) we finally concluded that for  $t$  large enough

$$\mathbb{P}(\tau_f > t) \sim \left( \frac{\mu}{\lambda_f} \right)^{k/2} \frac{1}{2\sqrt{\pi}(\mu\lambda_f)^{1/4}} \frac{k}{(\sqrt{\mu} - \sqrt{\lambda_f})^2} \frac{e^{-(\sqrt{\mu} - \sqrt{\lambda_f})^2 t}}{t^{3/2}}.$$

□

*Proof of Corollary 2.5 (b).* This immediate from the preceding computations and Remark 2.4. □

*Proof of Corollary 2.5 (c).* When  $\lambda_f = \mu$  (2.1) reads

$$\mathbb{P}(\tau_f > t) = \int_t^{+\infty} e^{-2\mu u} \frac{k}{u} I_k(2\mu u) du$$

using in turn inequalities (3.4) leads directly to the result. □

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